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Natural Regeneration of Subalpine Fir and Engelmann Spruce in Partially Harvested High-elevation Stands in East-Central British Columbia

O.A. Steen, R.A. Coupé, and
M.J. Waterhouse

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Ministry of Forests and Range
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ABSTRACT

This study examines factors affecting natural restocking of small (≤ 1 ha) openings created by partial harvesting of high elevation (> 1500 m) Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)–subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) stands in east-central British Columbia, Canada. We examined the effects of opening size (0.03, 0.13, and 1.0 ha), seedbed, and seed supply on density of post-logging regeneration for 10 years post-harvest. The effect of opening size on growth release of advance regeneration was also examined. Both seed production and seedbed limited densities of post-logging seedlings. Densities of subalpine fir and Engelmann spruce post-logging regeneration remained low at two sites where seedfall was low. Seedbed scarification significantly increased seedling densities where seed rain was high. In the absence of scarification, abundant seed production had little effect on post-logging seedling densities. Increased height and basal diameter growth of advance regeneration following logging was greater on 1.0-ha than 0.13-ha and 0.03-ha openings. This study demonstrates that post-logging natural regeneration in combination with advance regeneration can restock small openings in partially harvested stands where there is an adequate distribution of mineral soil seedbed and logging or site preparation coincide with or shortly precede a year of abundant seed production.

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The Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zone includes the highest-elevation forests of east-central British Columbia, lying beneath the alpine parkland and alpine tundra (Coupé et al. 1991). Industrial timber harvesting in these forests has been relatively recent, but since the late 1980s large-scale clearcut harvesting has expanded rapidly and currently extends to the highest elevations of the forest. As clearcutting has expanded, resource managers and the public have expressed concern about its effects on sustainability of timber production and maintenance of critical wildlife habitat (Eastham and Jull 1999; Vyse 1999; Lajzerowicz et al. 2006). Of special concern in east-central British Columbia is winter habitat for mountain caribou *(Rangifer tarandus caribou)*, an ecotype of woodland caribou that depends on high-elevation old forests and is at risk of extinction in British Columbia (Youds et al. 2000). Clearcut harvesting removes arboreal lichens on which caribou depend for winter forage (Youds et al. 2000). Extensive clearcutting concentrates suitable winter habitat into small areas, making caribou more susceptible to predation.

To maintain critical winter habitat for caribou while still extracting timber, a group selection silvicultural system, with openings no larger than 1.0 ha, has been recommended for large portions of the caribou winter range (Armleder and Stevenson 1996; Newsome et al. 2000; Youds et al. 2000). This partial harvesting system is also expected to maintain many other wildlife habitat values and to be more similar than clearcutting to the natural gap-phase disturbance regimes of these forests (Coxson et al. 2003; Delong and Meidinger 2003; Klenner and Sullivan 2003; Waterhouse et al. 2004).

Practicing foresters generally do not use natural regeneration in high-elevation Engelmann spruce–subalpine fir cutover sites because recruitment of post-logging natural regeneration is very slow in clearcuts, where distance from residual trees limits seedfall (Eastham and Jull 1999; LePage et al. 2000) and competing vegetation is often abundant. In addition, the greater abundance of subalpine fir compared with the more desirable Engelmann spruce in advance regeneration layers (Steen et al. 2005) and the high mortality of advance regeneration following logging (Parish and Antos 2005) discourage use of natural regeneration.

Although of limited value for restocking large clearcuts, natural regeneration may be a viable option for restocking small (< 1 ha) openings in high-elevation forests (Noble and Alexander 1977; Feller 1997, 1998; Eastham and Jull 1999; Greene et al. 1999; Eastham 2001; Parish and Antos 2005) created by group selection harvesting. Natural regeneration is usually abundant in mature forests of eastern British Columbia (Antos and Parish 2002; Steen et al. 2005), quickly restocks many disturbed areas such as roadsides, and can contribute significantly to restocking of cutover areas (Butt and Vyse 1992; Puttonen et al. 1997; Huggard and Vyse 2002). However, because most timber harvesting at high elevations of east-central British Columbia has occurred on relatively large clearcuts, experience with natural regeneration of small openings is very limited. A better understanding is needed of the potential for natural regeneration to restock small openings in high-elevation Engelmann spruce–subalpine fir forests (Feller 1998; Parish and Antos 2005).

Substantial information is available on the potential of natural regeneration to restock high-elevation Engelmann spruce–subalpine fir forests of the U.S. Rocky Mountains and in southern Alberta (Stahelin 1943; Day 1964, 1970; Roe and DeJarnette 1965; Alexander 1968, 1974, 1984, 1986; Noble and Alexander 1977; McCaughey et al. 1991; Shearer and Schmidt 1999). Although this information is broadly applicable to the high-elevation forests of British Columbia, differences of climate, soils, and vegetation require that the applicability of this information to British Columbia be tested in its high-elevation forests (Feller 1997).

This study was initiated in 1992, then followed for 10 years, to evaluate factors affecting natural restocking of small (≤ 1.0 ha) openings in partially harvested Engelmann spruce–subalpine fir forests of east-central British Columbia. The study is part of the larger Quesnel Highland Alternative Silvicultural Systems Project, which was initiated in 1992 to examine the effectiveness of a group selection system for maintaining mountain caribou winter habitat (Armleder and Stevenson 1996). In this project, timber was harvested from 33% of the area of each of three harvest blocks in small (0.03, 0.13, 1.0 ha) circular openings, distributed throughout the blocks. In the longer term, the proposed silvicultural system would harvest 33% of the area of each block once every 80 years, resulting in 240 years between reharvesting the same areas. The smallest opening size (0.03 ha,

r = 10 m) in the project was selected as the smallest opening that a feller-buncher can reasonably log. Because no portion of a small opening is more than 10 m from an opening edge, this opening size retains the most nearly continuous winter habitat for caribou within the block and it best emulates natural gap-based disturbances within the stands. The medium-sized openings (0.13 ha, r = 20 m) allow greater timber harvesting and silvicultural efficiencies with only modest increases in maximum distances from a residual forest edge. They are similar in size to many natural openings in the pre-harvest stands. The large openings size (1.0 ha, r = 56.4 m) is a maximum for group selection harvesting and offers an upper limit for assessing group selection opening size effects on regeneration, wildlife habitat, and microclimate.

The principal objectives of this study are (1) to evaluate the potential of post-logging natural regeneration to restock the small (0.03, 0.13, and 1.0 ha) openings; (2) to determine if small opening sizes, undisturbed seedbed, and seed supply limit the density of post-logging regeneration in partially harvested high-elevation Engelmann spruce–subalpine fir stands; and (3) to determine if the small opening sizes limit the growth of advance regeneration post-harvest.

STUDY AREA

Natural regeneration was measured on three partially harvested sites (Table 1) in the Engelmann Spruce–Subalpine Fir wet cold biogeoclimatic subzone, Cariboo variant (ESSFwc3) (Steen and Coupé 1997). The ESSFwc3 includes the highest-elevation forests in the Quesnel Highland, extending from about 1500 to 1800 m, where it borders alpine parkland or alpine tundra (Steen and Coupé 1997). The climate of this subzone variant is characterized by cold, snowy winters and cool, moist summers with approximately 1400 mm of precipitation annually and a mean annual temperature of –1.0°C (Farnden 1994; Steen and Coupé 1997). On the study sites, mean daily air temperatures during the growing season ranged from 5 to 15°C and soil temperatures at 15 cm below the surface ranged from 5 to 10°C (Stathers et al. 2001). Frequent precipitation is characteristic of the growing season as a result of afternoon convective rain

showers of 1–10 mm, three to five times per week (Stathers et al. 2001). Peak snowpack is most often 2–3 m, and snow is present on the ground from late October to early June. Soil temperatures remain near 0°C during the winter due to insulation by the snowpack (Stathers et al. 2001). Soils are mostly loamy skeletal Humo-Ferric Podzols developed in glacial till. Soil humus forms on mesic sites are typically hemimors and mormoders (Green et al. 1993) less than 8 cm thick.

TABLE 1 *Environmental features of the three study sites*

	Location	Area (ha)	Elevation (m)	Slope (%)	Slope aspect
Blackbear Creek	52°36′37″ N 121°10′52″ W	61	1450–1590	15–40	Northeast
Lower Grain Creek	121°24′30″ W 52°41′29″ N	40	1580–1700	15–35	Northwest
Upper Grain Creek	52°40′45″ N 121°12′02″ W	44	1460–1640	22–32	West

Pre-logging stands on all three sites were strongly dominated by subalpine fir in both the canopy and regeneration layers and by variable amounts of Engelmann spruce (Steen et al. 2005). The understorey on mesic sites was dominated by a nearly closed, low shrub layer consisting primarily of *Rhododendron albiflorum* Hook., *Vaccinium membranaceum* Dougl. ex Hook., and *Vaccinium ovalifolium* Sm. Common herbaceous species included *Rubus pedatus* J.E. Sm., *Streptopus lanceolatus* (Ait.) Reveal, *Valeriana sitchensis* Bong., *Tiarella trifoliata* L., and *Gymnocarpium dryopteris* (L.) Newman (Steen et al. 2005). These species were also common on harvested openings.

The three stands used in this study were initiated, probably following a wildfire, about 300, 430, and 450 years ago, respectively (Steen et al. 2005). Stands had deep, multi-layered canopies with trees up to 40 m tall. Density of stems < 12.5 cm and ≥ 12.5 cm dbh averaged 26 175 and 503 stems/ha, respectively. Eighty-six percent of all stems were subalpine fir. Regeneration of both species occurred primarily on decaying logs (Steen

et al. 2005), as is typical of other high-elevation Engelmann spruce–subalpine fir forests in British Columbia (Parish and Antos 2005).

METHODS

STUDY DESIGN AND TREATMENTS

We examined the effects of site (three harvest blocks), opening size (1.0, 0.13, and 0.03 ha), seedbed scarification (scarified, not scarified), and artificial seeding (seeded, not seeded) on density of subalpine fir and Engelmann spruce post-logging regeneration. We also examined growth of subalpine fir and spruce advance regeneration in the three opening sizes without scarification or seeding treatments. The study was initiated as a randomized block split-split plot design with opening size as the main plot factor, the three sites as randomized replicates of the ESSFwc3 study area, and scarification and seeding treatments as split-plot factors.

The three sites were required to be on west- to north- or east-facing slopes, to have a general slope grade of 15–40%, and to be predominantly well or moderately well drained. South-facing slopes were avoided because operational experience at the time suggested less severe regeneration challenges on these warmer slopes. Each site was subdivided into four treatment units of approximately equal size (10–15 ha). Three harvest opening–size treatments and an unharvested treatment were randomly assigned to each treatment unit. Each of the harvest treatments removed timber from one-third of the treatment unit area in small circular openings (0.03, 0.13, or 1.0 ha) and connecting trails (approximately 4 m wide). Timber was harvested in winter 1992/93 using a feller-buncher and grapple skidder on a 1- to 2-m snowpack.

Fifteen openings on each of the three sites were randomly selected for study. These included eight openings in the small (0.03 ha), four openings in the medium (0.13 ha), and three openings in the large (1.0 ha) opening-size treatments. All openings selected for study were required to have a predominantly mesic ecological soil moisture regime and representative levels of logging disturbance.

Four regeneration monitoring plots (2 × 3 m) were located in each of the eight small openings, eight in each of the four medium openings, and 11 in each of the three large openings, for a total of 97 plots on each of the three sites. Regeneration plots were located at random bearings and at the square of random distances from opening centre to ensure that all areas of the opening had equal probability of being represented. No data were collected from the unharvested treatment.

Each regeneration plot was subdivided into two split plots, each 2 × 1 m and separated by an approximate 1-m buffer. Scarification treatments (scarified, not scarified) were randomly assigned to each split plot. Each split plot was further subdivided into two 1 × 1 m microplots (split-split plots) and the more downslope microplot was seeded by hand with subalpine fir and Engelmann spruce. Thus, each 2 × 3 m plot included the following 1 × 1 m microplot treatments:

- scarified, seeded (SS),
- scarified, not seeded (SN),
- not scarified, seeded (NS), and
- not scarified, not seeded (NN).

Scarification during the first season following logging (July/August 1993) removed virtually all above-ground vegetation and forest floor layers to a depth of approximately 10 cm. The artificial seeding treatment consisted of sowing subalpine fir and Engelmann spruce seed in late fall in each of 4 years from 1993 to 1996. Ten subalpine fir and 10 spruce seed were covered each year with about 0.5 cm of soil to minimize rodent predation. The B.C. Ministry of Forests seed laboratory supplied high-viability seed, which was collected within the same region and from a similar elevation as the study sites. Germinants from artificial and natural seeding were not distinguished.

FIELD MEASUREMENTS

Natural seedfall was sampled from 1994 to 1997 by systematically locating 16 seed traps (0.5 × 0.5 m) in one large opening at each of the three sites. Seed traps were not located in medium or small openings. Seed traps were placed at distances of 10, 30, 40, and 50 m in each of the four cardinal directions from opening centre (approximately 46, 26, 16, and 6 m from the residual

stand edge, respectively). Traps were emptied once each year in June or July and seed was cut to determine numbers of filled and unfilled seed of spruce and fir.

At each microplot, potential seedling substrate was assessed by estimating the percentage of microplot surface covered by mineral soil, moss, rock, tree roots (> 3 cm diameter), fine woody debris (< 3 cm diameter), woody debris (≥ 3 cm diameter) by decay class (Maser et al. 1988), and undisturbed forest floor. Vegetation descriptions at each microplot included visual estimates of the percentage of the microplot surface covered by tall (> 100 cm) shrubs, low (25–100 cm) shrubs, tall herbs, low herbs, all plants ≥ 25 cm tall, and all vascular plants < 25 cm tall.

Numbers of live subalpine fir and Engelmann spruce stems were monitored on each of the 1 × 1 m microplots in the fall following plot scarification (1994) and in 1995, 1996, 1997, 1999, and 2003. Stems were tallied by substrate type (first 3 years only) and by the following three age/height categories: < 1 year old (current year germinant), ≥ 1 year old but < 7 cm tall, and 7–130 cm tall. Stems > 130 cm tall, which were uncommon, were not tallied. Stems < 1 year old were estimated as those having no evidence of a previous terminal bud and by the frequent presence of seed leaves. Stems > 1 year old in 1994 were considered to be advance regeneration and were subtracted from total densities in later years to estimate post-logging regeneration density.

Advance regeneration density and height growth were sampled separately from the microplot studies on six small, three medium, and two large randomly selected openings on each site in the first season after logging (1993). All stems 30–130 cm tall within a 1 m wide transect across each opening were tallied by species, height, basal diameter, and logging damage. Up to 40 stems of subalpine fir and Engelmann spruce 30–130 cm tall and with little or no logging damage were selected in 1993 for growth measurements from throughout each selected opening. Stems were tagged in 1993 and relocated and remeasured in 2001.

OPERATIONAL REGENERATION SURVEY

A standard operational regeneration survey, consistent with B.C. Ministry of Forests standards and procedures for the area, was conducted in spring 2001 (beginning of year 8 post-harvest) to determine if natural regeneration was sufficient to meet minimum legislated regeneration stocking requirements for

these forests. The standards required 700 well-spaced stems/ha of the preferred (subalpine fir and interior spruce) plus acceptable (lodgepole pine) species and 600 well-spaced stems/ha of the preferred species. To be considered well spaced, each tallied stem had to be ≥ 2 m from another tallied stem and ≥ 15 cm tall. For this study, however, two surveys were conducted: the first used a height of 15 cm and the second a height of 10 cm. These surveys did not distinguish between post-logging regeneration and advance regeneration.

DATA ANALYSES

Although the study was initiated as a randomized block design, significant fixed factors related to elevation and topography were not recognized in the initial selection of sites and there was a significant site–scarification interaction effect on regeneration densities. As a result, in all analyses of post-logging regeneration density, site was treated as a fixed factor in a factorial design. Interpretations of opening size, scarification, and seeding effects on post-logging natural regeneration are therefore necessarily restricted to the three study sites. Growth of advance regeneration stems, all of which occurred on unscarified areas, was analyzed with site as a random factor.

The effects of site, opening size, scarification, and artificial seeding and their interactions on post-logging regeneration density of Engelmann spruce and subalpine fir were tested by ANOVA using the SAS Mixed Procedure (SAS Institute Inc. 2003). Because regeneration densities in microplots had many zero values and a strongly skewed distribution, all analyses were conducted on opening mean densities. Regeneration densities were averaged by species and age/height class for each of the 45 openings before analyses. Planned contrast analyses tested the following hypotheses regarding post-logging regeneration density:

- mean density in large openings minus mean density in medium and small openings = 0; and
- mean density in medium openings minus mean density in small openings = 0.

Unplanned comparisons between individual site, opening size, scarification, and seeding treatment combinations were tested by Scheffé's method for multiple comparisons (Sokal and Rohlf 1995) when main ANOVA model treatment effects were significant. In all tests, differences were considered statistically significant at $\alpha = 0.05$.

Uniformity of substrate and vegetation conditions between sites and opening sizes were tested separately for scarified and unscarified treatments by ANOVA or log-linear analyses of plot averages.

Seedfall data (numbers of filled seed/m^2 of subalpine fir and Engelmann spruce) were summarized for each of the 4 years of sampling but only data from the 1993 seedfall were analyzed for effects of site. Seedfall in other years was too low to analyze and contributed little to total seedfall during the monitoring period.

Opening-size effects on height growth of advance regeneration were assessed using a randomized block design with site as a random factor and opening size as the only fixed factor. The analyses used the difference between mean annual pre-logging (1991–1993) and mean annual post-logging (1999 and 2001) height increment as dependent variables. Height increment data from 2000 were not included because 2-year-cycle spruce budworm (*Choristoneura biennis* Freeman) attacked stem leaders in the summer before fall measurement in that year. Stem basal area growth response was tested by analyzing the change in basal area between 1993 and 2002. Magnitude of changes may be conservative due to possible growth losses resulting from 2001 budworm attack. Height and basal area were analyzed separately by species and height class (30–80 and 81–130 cm tall) combinations. All tests were based on remeasurement of tagged stems.

RESULTS

SEEDBED UNIFORMITY

Post-logging seedbed characteristics were very similar among the sites and opening sizes. On unscarified plots, forest floor formed the predominant (> 67%) seedbed on all sites, and there were no significant site ($P = 0.14$), opening size ($P = 0.30$), or site × opening size interaction ($P = 0.51$) effects on percentage of seedbed formed by forest floor. On scarified plots, mineral soil formed the predominant (> 74%) seedbed on all sites and treatments. The mean percentage of seedbed formed by soft woody debris was very similar among the three sites and the three opening sizes (6–7% by site and 4–7% by opening size on unscarified plots; ≤ 1% by both site and opening size on scarified plots).

SEEDFALL

An average of 45 (s.d. = 27) subalpine fir and 167 (s.d. = 49) Engelmann spruce filled seeds/m^2 were collected from the Blackbear Creek seed traps in summer 1994 (seed matured in 1993). In the subsequent 3 years at this site, average subalpine fir and spruce seedfall density ranged from 0.0 to 4.5 and 1.0 to 7.3 seeds/m^2 per year, respectively. On the Upper and Lower Grain Creek sites, seedfall densities in 1994 were less than one-tenth of the amount at Blackbear Creek (0.3 subalpine fir and 3.8 spruce seeds/m^2 at Upper Grain Creek; 4.0 subalpine fir and 7.8 spruce seeds/m^2 at Lower Grain Creek). Over the next 3 years, the average seedfall density in each year was < 1.0 subalpine fir seeds/m^2 and < 1.5 Engelmann spruce seeds/m^2. Seedfall was not quantitatively monitored after the first 4 years of the study, but observations indicate that seedfall increased marginally in 2003 (seed matured in 2002).

POST-LOGGING REGENERATION

On the Blackbear Creek site, subalpine fir was the most abundant species of post-logging tree regeneration during all years of monitoring. Subalpine fir densities at this site ranged from 16 stems/m^2 in 1994 to 4 stems/m^2 in 2003 (Figure 1), while Engelmann spruce densities ranged from 6 to 1 stems/m^2

(Figure 2). At the Lower Grain Creek and Upper Grain Creek sites, however, mean densities of subalpine fir and Engelmann spruce were very similar and averaged less than 1 stem/m^2 in all years.

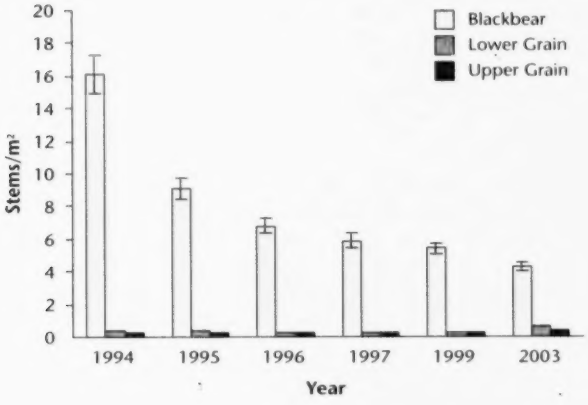

FIGURE 1 *Mean density (± 1 s.e.) of post-logging subalpine fir natural regeneration, all treatments combined.*

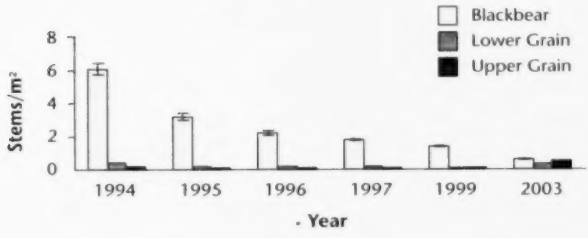

FIGURE 2 *Mean density (± 1 s.e.) of post-logging Engelmann spruce natural regeneration, all treatments combined.*

Most spruce and subalpine fir seedlings ≥ 1 year old on unscarified microplots in 1997 were on forest floor materials, with a lesser percentage on woody debris and mineral soil (Table 2). However, the greatest concentration (percentage of seedlings on substrate divided by percentage of substrate available) of subalpine fir seedlings was on woody debris ≥ 3 cm diameter, and the greatest concentration of Engelmann spruce seedlings was on mineral soil, followed by woody debris (Table 2). The percentage of seedlings on forest floor was essentially equal to the availability of forest floor substrate.

TABLE 2 *Distribution of seedlings ≥ 1 year old and < 7 cm tall in 1997 by substrate type on unscarified microplots*[a]

	Mean % cover	**Mean % of seedlings**		**Mean seedling concentration**[b]	
		Spruce	Fir	Spruce	Fir
Forest floor	70.1	67.5	70.1	0.96	1.00
Woody debris ≥ 3 cm diam	11.4	20.0	27.1	1.75	2.38
Mineral soil	3.9	12.8	2.8	3.28	0.72
Other	14.7	0	0	0	0

[a] Substrate percentages as of 1994.
[b] Concentration = % of seedlings on substrate/% cover of substrate on plot.

Site had a statistically significant effect on accumulated densities of both subalpine fir and Engelmann spruce post-logging regeneration, with P-values < 0.01 in all years, (except 2003, when the P-value for spruce density was 0.04) (Table 3). Mean densities of both species were consistently greater at Blackbear Creek than at either the Lower Grain Creek or Upper Grain Creek (Figures 1 and 2) sites. These greater densities reflected abundant germinants in the first year (1994) of the study (Table 4), immediately following the year of abundant seedfall at Blackbear Creek. After 1994, densities of new germinants of both Engelmann spruce and subalpine fir were extremely low at all sites until 2003 when a few more germinants, especially spruce, were recorded on the two Grain Creek sites (Table 4).

TABLE 3 *ANOVA P-values for assessing site and treatment effects on 10th-year (2003) mean density of post-logging subalpine fir and Engelmann spruce seedlings*

		P-values	
Source	**d.f.**	**Fir**	**Spruce**
Site (S)	2,36	<0.001	0.043
Opening size (O)	2,36	0.503	0.364
S × O	4,36	0.599	0.189
Scarification (C)	1,108	<0.001	<0.001
Seeding (E)	1,108	0.451	0.361
C × E	1,108	0.745	0.886
S × C	2,108	<0.001	<0.001
S × E	2,108	0.591	0.944
S × C × E	2,108	0.756	0.802
O × C	2,108	0.086	0.562
O × E	2,108	0.619	0.988
O × C × E	2,108	0.975	0.558
S × O × C	4,108	0.053	0.371
S × O × E	4,108	0.917	0.605
S × O × C × E	4,108	0.856	0.904
Large vs. medium/small openings	1,36	0.245	0.314
Medium vs. small openings	1,36	0.887	0.409

TABLE 4 *Mean (and s.d.) density (stems/m²) of subalpine fir and Engelmann spruce germinants (< 1 year old) during 6 years between 1994 and 2003 at each of the three sites*

	Subalpine fir						Engelmann spruce					
Site	**1994**	**1995**	**1996**	**1997**	**1999**	**2003**	**1994**	**1995**	**1996**	**1997**	**1999**	**2003**
Blackbear Creek	16.1	0.12	0.01	0.01	0.01	0.01	6.14	0.27	0.03	0.03	0.06	0.01
	(16.4)	(0.45)	(0.09)	(0.09)	(0.09)	(0.07)	(6.08)	(0.69)	(0.19)	(0.19)	(0.36)	(0.10)
Lower Grain Creek	0.36	0.11	0.01	0.01	0.00	0.04	0.44	0.14	0.08	0.08	0.00	0.16
	(0.75)	(0.43)	(0.11)	(0.11)	(0)	(0.19)	0.94	(0.54)	(0.35)	(0.36)	(0)	(0.45)
Upper Grain Creek	0.19	0.04	0.01	0.01	0.00	0.08	0.16	0.09	0.01	0.01	0.00	0.31
	(0.50)	(0.25)	(0.10)	(0.09)	(0)	(0.32)	(0.58)	(0.41)	(0.09)	(0.11)	(0)	(0.67)
	ANOVA test statistics for site effects											
F:	136.1	n/a	n/a	n/a	n/a	7.2	159.2	n/a	n/a	n/a	n/a	24.3
d.f.:	2,36					2,36	2,36					2,36
P:	<0.01					<0.01	<0.01					<0.01

n/a = ANOVA not completed due to few non-zero values for one or more sites.

Mortality of regeneration at the two Grain Creek sites was apparently smaller than at Blackbear Creek. By the 10th year of the study (2003), densities of Engelmann spruce at Blackbear Creek approached those at the Lower Grain Creek and Upper Grain Creek sites (Figure 2) even though initial densities were much greater. Tenth-year (2003) densities of subalpine fir remained significantly greater at Blackbear Creek than at either Lower Grain Creek ($T = 4.71$, d.f. = 36, $P < 0.01$) or Upper Grain Creek ($T = 5.22$, d.f. = 36, $P < 0.01$) sites.

Opening size had no significant effect on 10th year (2003) accumulated density of subalpine fir or Engelmann spruce post-logging regeneration (Table 3). At the Blackbear Creek site, mean density of post-logging subalpine fir seedlings tended to be greatest on medium openings (2.7, 6.0, and 4.4 stems/m^2 on large, medium, and small openings, respectively) while Engelmann spruce densities differed little among opening sizes (1.4, 1.3, and 1.3 stems/m^2 on large, medium, and small openings, respectively). At the Lower Grain Creek site, mean density differences among opening sizes were slight (0.3, 0.4, and 1.0 subalpine fir stems/m^2 and 0.1, 0.3, and 0.5 Engelmann spruce stems/m^2 on large, medium, and small openings, respectively). Densities at Upper Grain Creek were very similar to those at Lower Grain Creek.

Seedling densities in 1994 on scarified, unseeded microplots were compared with distance of microplot from residual stand edge to determine if distance in the large openings limited seedling numbers. Only data from large openings were used to include the greatest range of distances in the assessment. In addition, only data from the Blackbear Creek site were used. Although subalpine fir densities tended to decline with distance, relatively high densities were present up to about 35 m from the stand edge (Figure 3). Spruce densities showed little relationship to distance (Figure 4). There was no apparent relationship between seedling density and direction of microplot from opening centre.

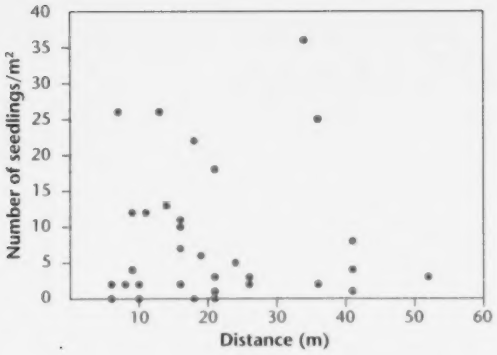

FIGURE 3 *Density of subalpine fir seedlings in 1994 on scarified, unseeded microplots in Blackbear Creek large openings versus distance of microplots from residual stand edge.*

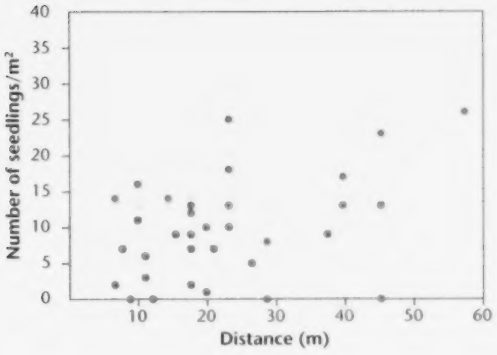

FIGURE 4 *Density of Engelmann spruce seedlings in 1994 on scarified, unseeded microplots in Blackbear Creek large openings versus distance of microplots from residual stand edge.*

Scarification had a significant effect on 10th year (2003) accumulated density of both subalpine fir and Engelmann spruce, including a strong interaction effect with site (Table 3). At the Blackbear Creek site, scarification significantly increased densities of both subalpine fir ($T = 15.6$, d.f. = 108, $P < 0.01$) and Engelmann spruce ($T = 9.2$, d.f. = 108, $P < 0.01$) with five times the mean number of fir seedlings and several times the mean number of spruce seedlings on scarified compared with unscarified microplots (Table 5). However, there was no significant scarification effect on seedling densities at either Lower Grain Creek ($P = 0.94$ for subalpine fir and 0.73 for spruce) or Upper Grain Creek ($P = 0.99$ for subalpine fir and 0.54 for spruce).

TABLE 5 *Mean (and s.d.) density (stems/m²) of post-logging subalpine fir and Engelmann spruce seedlings on scarified (SC) and unscarified (USC) microplots in 2003. Seeding treatments are combined.*

	Fir		Spruce	
	SC	USC	SC	USC
Blackbear Creek	7.4	1.3	1.0	0.1
	(8.6)	(3.0)	(1.7)	(0.6)
Lower Grain Creek	0.7	0.5	0.4	0.2
	(1.2)	(1.1)	(0.8)	(0.5)
Upper Grain Creek	0.3	0.4	0.6	0.4
	(0.7)	(1.2)	(1.0)	(0.9)

On unscarified microplots, the 2003 mean density of subalpine fir seedlings (Table 5) did not differ significantly between Blackbear Creek and either Lower Grain Creek ($P = 0.94$ for subalpine fir and spruce) or Upper Grain Creek ($P = 0.91$ for subalpine fir and 0.08 for spruce) sites. That is, the significantly greater densities of fir on Blackbear Creek than on the two Grain Creek sites occurred only on the scarified microplots.

In 2003, 82% of the scarified microplots and 30% of the unscarified microplots on the Blackbear Creek site contained at least two post-logging seedlings (Engelmann spruce or subalpine fir) ≥ 1 year old or at least one post-logging seedling ≥ 7 cm

tall. In contrast, only 16–18% of the scarified and unscarified microplots at the Lower and Upper Grain Creek sites were similarly stocked.

Artificial seeding in the first 4 years of the study (1994–1997) had no significant effect on 10th-year (2003) densities of subalpine fir or Engelmann spruce post-logging regeneration (Table 3). In all years before year 6 (1999), artificial seeding significantly increased seedling densities at the Upper Grain Creek and Lower Grain Creek sites, but a significant effect did not persist, due to variability among plots and apparently the swamping effects of natural seed rain. Artificial seeding had no significant effect on seedling densities at Blackbear Creek in any year, apparently because the heavy 1993 seed rain swamped the effect of artificial seeding.

ADVANCE REGENERATION

Mean density of advance regeneration 30–130 cm tall (Engelmann spruce and subalpine fir combined) on the sample transects in the year following logging ranged from 739 stems/ha on the Blackbear Creek site to 3476 stems/ha on the Upper Grain Creek site (Table 6). Subalpine fir density was 2.3–10 times that of Engelmann spruce. On the unscarified microplots in the year following logging, mean density of all advance regeneration < 130 cm tall, including that < 30 cm tall, ranged from 3410 stems/ha at Blackbear Creek to 6600 and 6900 stems/ha at Upper and Lower Grain Creek sites, respectively.

TABLE 6 *Mean (and s.d.) density of subalpine fir and Engelmann spruce advance regeneration 0.3–1.3 m tall in 1994*

	Density (stems/ha)
Blackbear Creek	
Fir	615 (646)
Spruce	124 (184)
Lower Grain Creek	
Fir	2402 (1423)
Spruce	270 (283)
Upper Grain Creek	
Fir	2428 (2223)
Spruce	1048 (1181)

Of the 443 advance regeneration stems tagged in 1993 for growth measurements, 86% survived to 2001. The rate of mean annual height growth tended to increase following logging, especially on large openings (Figures 5 and 6). Opening size had a significant effect on height growth increments of subalpine fir 30–80 cm tall, but not of subalpine fir 81–130 cm tall, spruce 30–80 cm tall, or spruce 81–130 cm tall (Table 7). Post-logging height growth increases were greater in the large than the medium and small openings for spruce 30–80 cm tall, spruce 81–130 cm tall, and subalpine fir 30–80 cm tall, but not subalpine fir 81–130 cm tall (Table 7). Height growth increases did not differ significantly between the medium and small openings for any species/height class combination.

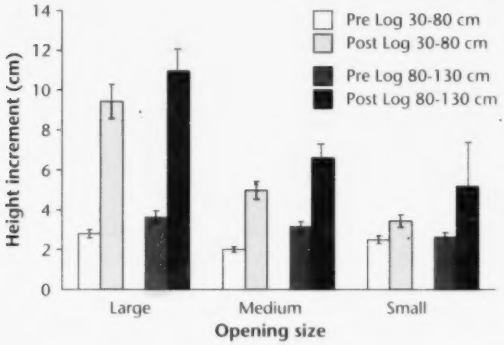

FIGURE 5 *Mean annual height increment of pre-logging (1990–1992) and post-logging (1999, 2001) subalpine fir advance regeneration. Height class is based on height in 1993.*

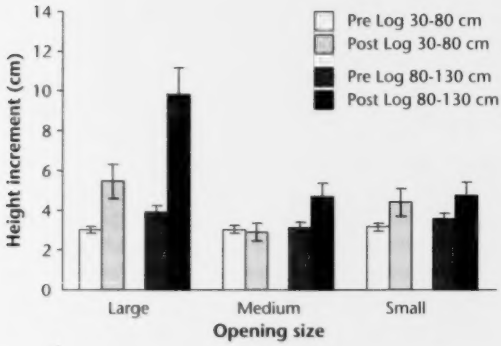

FIGURE 6 *Mean annual height increment of pre-logging (1990–1992) and post-logging (1999, 2001) Engelmann spruce advance regeneration. Height class is based on height in 1993.*

TABLE 7 *ANOVA P-values for assessing opening size (L, M, S) effects on mean annual height and basal diameter growth of subalpine fir and Engelmann spruce advance regeneration. Height classes of stems are heights in 1993.*

		Fir		Spruce	
Source	d.f.	30–80 cm	81–130 cm	30–80 cm	81–130 cm
		Height growth			
Opening size main effect	2,4	0.045	0.316	0.076	0.081
L vs. M/S openings	1,4	0.021	0.159	0.034	0.038
M vs. S openings	1,4	0.350	0.764	0.278	0.846
		Basal diameter growth			
Opening size main effect	2,4	0.053	0.008	0.051	0.040
L vs. M/S openings	1,4	0.025	0.004	0.021	0.019
M vs. S openings	1,4	0.395	0.126	0.675	0.964

Basal diameter of live subalpine fir and Engelmann spruce advance regeneration increased markedly following logging, especially in large openings (Figures 7 and 8). Opening size had a significant effect on the magnitude of differences for spruce 30–80 cm tall, spruce 81–130 cm tall, subalpine fir 30–80 cm tall, and subalpine fir 81–130 cm tall (Table 7). Stem diameter increases were significantly greater in large than in medium and small openings but were not significantly different between medium and small openings for any species/height combination (Table 7).

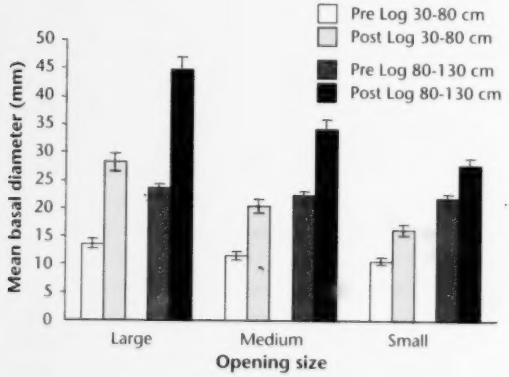

FIGURE 7 *Mean (±1 s.e.) basal diameter of subalpine fir advance regeneration in 1993 (pre-log) and 2003 (post-log). Height classes are based on height in 1993.*

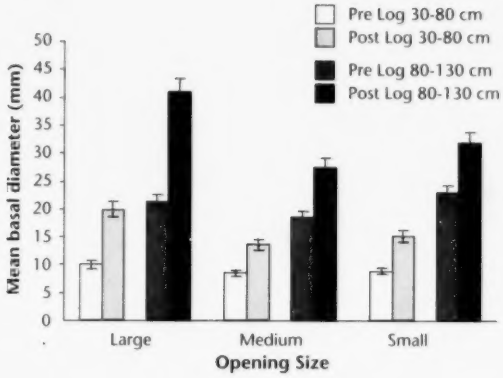

FIGURE 8 *Mean (±1 s.e.) basal diameter of Engelmann spruce advance regeneration in 1993 (pre-log) and 2003 (post-log). Height class is based on height in 1993.*

OPERATIONAL REGENERATION SURVEY

None of the opening size treatments had the required number of well-spaced stems that were ≥ 15 cm tall by the beginning of year 8 following logging. Mean number of stems/ha of well-spaced subalpine fir ≥ 15 cm tall ranged from 271 at Upper Grain Creek to 398 at Blackbear Creek. Mean number of Engelmann spruce ranged from 0 at Lower Grain Creek to 144 at Upper Grain Creek. When minimum height was reduced to 10 cm, only the small openings at Blackbear Creek had the required number of acceptable stems.

DISCUSSION AND MANAGEMENT IMPLICATIONS

The results of this study show that logged openings of ≤ 1.0 ha in high-elevation Engelmann spruce–subalpine fir forests can be regenerated by post-logging seedlings, provided that logging or site preparation coincides with or shortly precedes abundant seed production, and provided that suitable seedbed (especially mineral soil but also decaying wood) is present. On the Blackbear Creek site, 10th-year natural regeneration stocking, including all stems > 1 year old without any height requirement, exceeded the stocking that would result from 2 × 2 m grid planting. However, natural regeneration at the study sites was slower than required by regeneration standards, and by year 8 few seedlings had reached the height required by standards. Regeneration stocking standards in British Columbia and elsewhere are designed primarily for timber emphasis silvicultural systems with a defined harvest rotation of 120 years or less. The group selection system proposed for maintaining caribou habitat within the study area is based on a harvest rotation age of 240 years. That is, the amount of time available to regenerate a mature stand is at least twice as long as under "normal" practices. As a result, slow natural regeneration establishment and growth, similar to that in this study, would be expected to have little impact on timber production. Parish and Antos (2005) concluded that natural regeneration, possibly in combination with infill planting, is a viable option for restocking 1.0-ha patch cuts within high-elevation Engelmann spruce–subalpine fir forests in south-central British Columbia.

Seed production variations had a substantial effect on seedling densities in this study. During 4 years of monitoring seedfall and 6 years of monitoring numbers of new germinants, abundant seed was produced during only 1 year (1993) on one site (Blackbear Creek) and germinants were abundant only following the peak seed production. The effect of seed production variations was evident in total seedling densities for several years following the year of peak production, suggesting that seed production variation is a primary factor limiting post-logging regeneration. This conclusion is consistent with other studies of high-elevation Engelmann spruce–subalpine fir forests in the western United States and British Columbia (Alexander 1986; Coates et al. 1994; Eastham and Jull 1999). However, Parish and

Antos (2005) describe a more consistent year-to-year recruitment of seedlings in small (1.0 ha) logged openings at high elevations in southeastern British Columbia with some germinants recorded in every year.

Smaller seed production recorded at the two Grain Creek sites compared with the Blackbear Creek site may be related to environmental differences between the sites. Seed production and frequency of peak seed years have been reported to decrease with increasing elevation in the Engelmann spruce–subalpine fir forests of British Columbia (Farnden 1994). Although the elevation of the three sites does not differ greatly, the two Grain Creek sites occur beneath large alpine areas that are sources of cold air and snow meltwater, which, together with later-lying snow, result in shorter growing seasons and colder soils in the early growing season (Stathers et al. 2001; Lajzerowicz et al. 2006). In contrast, the Blackbear Creek site is near the upper slopes of a ridge without a large alpine or snowfield area above, and snow disappears earlier in the spring (Stathers et al. 2001; Lajzerowicz et al. 2006). Soil temperatures at 15 cm below the surface in large openings were consistently higher at the Blackbear Creek site than at either of the two Grain Creek sites (Stathers et al. 2001). The effects on seed production of a shorter growing season with colder early-season soils may be similar to the effects of higher elevations. Colder soils may also reduce survival and initial growth of Engelmann spruce seedlings (DeLucia 1986; DeLucia and Smith 1987; Balisky and Burton 1997). Lower survival and growth of planted Engelmann spruce and subalpine fir on the two Grain Creek sites than on the Blackbear Creek site may also reflect these environmental differences (Lajzerowicz et al. 2006). Additional studies are needed to clarify the effects of large upslope topographic differences on soil and air temperatures and subsequent seed production and seedling establishment.

Seedbed scarification, combined with vegetation removal, significantly increased 10th-year post-logging establishment of both Engelmann spruce and subalpine fir, when seedfall was abundant (i.e., at Blackbear Creek). Several studies have shown that exposed mineral soil promotes greater seedling establishment and growth, especially of spruce, due to more favourable moisture and temperature conditions (Smith and Clark 1960; Eis 1965; Alexander 1986; Butt and Vyse 1992; Coates et al. 1994; Balisky and Burton 1997; Feller 1998; Eastham and Jull 1999;

LePage et al. 2000; Wang and Kemball 2005). Eastham and Jull (1999) studied seed dispersal and the effects of seedbed scarification and direct seeding on density of Engelmann spruce and subalpine fir germinants in two partial-cut treatments. Suitable seedbed in the partial cuts limited the number of germinants. The authors concluded that opportunities to use post-logging natural regeneration for restocking cutover areas could be increased by anticipating seed production from cone crop assessments and applying seedbed treatments before heavy seedfall. Seed and seedling pathogens in the forest floor may also limit seedling establishment (Zhong and van der Kamp 1999).

In the absence of scarification, the high seedfall differences between sites in this study had no significant effect on 10th-year densities of Engelmann spruce or subalpine fir regeneration. That is, suitable seedbed is a primary factor limiting seedling establishment and is necessary for greater seedfall to be reflected in greater seedling densities.

Analyses of Engelmann spruce and subalpine fir seedling distributions on unscarified plots suggest that both species establish better on decaying wood than on undisturbed forest floor. That is, the proportion of seedlings relative to the substrate availability was greater for decaying wood than for forest floor. Several studies have documented abundant regeneration on decaying wood in high-elevation forests (Oosting and Reid 1952; Day 1964; Knapp and Smith 1982; Little et al. 1994; Antos et al. 2000; Brang et al. 2003; Mori et al. 2004; Steen et al. 2005; Parish and Antos 2005). Conservation and continued input of woody debris following logging should increase success and reliability of natural regeneration after subsequent harvests.

The range of opening sizes (0.03–1.0 ha) included in this study had no statistically significant effect on density of post-logging regeneration of either Engelmann spruce or subalpine fir. In large openings, seedling densities of subalpine fir tended to decline with distance, especially beyond 40 m, but spruce densities showed little relationship to distance from residual stand edge up to 50 m. Because the location of plots in this study was weighted to increase the number of plots towards the opening perimeter (in proportion to increase in opening area), seed rain declines with distance had less effect on average plot density within the opening. Seed dispersal studies in the United States suggest that 30–50% of Engelmann spruce seed falls more than 30 m from the windward side of a stand edge

(Alexander 1986; Coates et al. 1994). Subalpine fir has a larger, heavier seed than Engelmann spruce and most seed falls within 60 m of the parent tree (Owens and Molder 1985). Coates (2002) also found little effect of a range of gap sizes (0.002–0.5 ha) on seedling recruitment following harvesting in northwest British Columbia. Huggard and Vyse (2002) measured significantly fewer seedlings in 10- and 1-ha openings than in 0.1-ha openings or in individual tree selection treatments. They concluded that opportunities for natural regeneration are greater in 0.1-ha than in 1- or 10-ha openings.

The absence of a significant reduction in density of subalpine fir seedlings in the smallest (0.03 ha) openings compared with the medium (0.13) or large (1.0 ha) openings is not surprising since fir establishes abundantly even below an undisturbed forest canopy (Parish and Antos 2005; Steen et al. 2005). Engelmann spruce establishment, however, is limited by canopy closure in undisturbed stands (Steen et al. 2005), and small openings might be expected to have greater effect on spruce than subalpine fir establishment. However, the smallest openings in this study (0.03 ha, radius = 10 m) did not have significantly fewer seedlings than the 1.0-ha openings. Growth of Engelmann spruce and subalpine fir seedlings has been noted to be greater in clearcuts than in open or closed forests (Feller 1998).

Reliance on natural regeneration rather than planted stock requires greater attention to seed production and dispersal, seedbed conditions, and microclimate (Alexander 1984; Weetman and Vyse 1990; McCaughey et al. 1991). Engelmann spruce may produce abundant seed every 2–6 years (Fowells [compiler] 1965) on some sites, but the size and frequency of cone crops generally decrease with increasing elevation (Coates et al. 1994). High-elevation stands in British Columbia are estimated to have peak cone crops on average only once every 12 years (B.C. Ministry of Forests 1990), possibly in response to dry summers followed by moist springs (Eastham and Jull 1999). Engelmann spruce–subalpine fir forests such as the two Grain Creek sites, which receive cold air and abundant snowmelt water from large upslope alpine areas, may have especially reduced frequency of peak cone crops. However, the significance to natural regeneration success of infrequent years of peak seed production needs to be examined in the context of the relatively continuous establishment of new seedlings in undisturbed stands of this study (Steen et al. 2005) and in southeastern British Columbia

(Antos et al. 2000), and the moderately consistent year-to-year presence of germinants recorded in small (1 ha) openings at Sicamous Creek in southeastern British Columbia (Parish and Antos (2005). Due to seed production variations and significant environmental differences among sites at these high elevations, post-logging natural regeneration rates will likely be more variable than at lower elevations.

Advance regeneration can contribute substantially to reforestation of small openings in high-elevation Engelmann spruce–subalpine fir forests, and damage of stems during logging should be minimized when relying on natural regeneration. Before logging, densities of stems < 2.0 m tall were > 4000 stems/ha in the Blackbear Creek stand and > 30 000 stems/ha in the two Grain Creek stands (Steen et al. 2005). Although densities were substantially reduced during logging, survival of advance regeneration stems 0.3–1.3 m tall in the 8 years following logging was nearly 90%.

Greater growth release of advance regeneration in the 1.0-ha openings compared with the 0.03- or 0.13-ha openings is consistent with differences in planted seedling growth on similar-sized openings (Lajzerowicz et al. 2004, 2006). Lajzerowicz et al. (2004) attributed increased growth on larger openings to more available light and warmer soils. Growth of Engelmann spruce and other conifers is generally greatest in full or nearly full sunlight and increases with level of canopy removal (McCaughey and Schmidt 1982; Wright et al. 1998; Coates and Burton 1999; Coates 2000), although complete canopy removal has short-term (1–7 years) negative effects on subalpine fir height growth compared with partial cuts (Krasowski and Wang 2003). Wright et al. (2000) concluded that shade-tolerant species such as subalpine fir show little or no effect of previous periods of suppression on growth response to increased light. Although shading from shrub vegetation may limit growth in this study (see Bassman et al. 1992), shrubs would not account for growth rate differences between opening sizes because mean shrub cover differed little between opening sizes (M. Waterhouse, B.C. Min. For. Range, Williams Lake, B.C., unpublished data). Mean annual height growth in the large opening of this study exceeded that recorded by Parish and Antos (2005), but their study included smaller stems.

LITERATURE CITED

Alexander, R.R. 1968. Natural reproduction of spruce-fir after clearcutting in strips, Fraser Experimental Forest. U.S. Dep. Agric. For. Serv., Res. Note RM-101.

_____. 1974. Silviculture of subalpine forests in the central and southern Rocky Mountains: the status of our knowledge. U.S. Dep. Agric. For. Serv., Res. Pap. RM-121.

_____. 1984. Natural regeneration of Engelmann spruce after clearcutting in the central Rocky Mountains in relation to environmental factors. U.S. Dep. Agric. For. Serv., Res. Pap. RM-254.

_____. 1986. Engelmann spruce seed production and dispersal, and seedling establishment in the central Rocky Mountains. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. RM-134.

Antos, J.A. and R. Parish. 2002. Structure and dynamics of a nearly steady-state subalpine forest in south-central British Columbia, Canada. Oecologia 130:126–135.

Antos, J.A., R. Parish, and K. Conley. 2000. Age structure and growth of the tree-seedling bank in subalpine spruce-fir forests of south-central British Columbia. Am. Midl. Nat. 143:342–354.

Armleder, H.M. and S.K. Stevenson. 1996. Using alternative silvicultural systems to integrate mountain caribou and timber management in British Columbia. Rangifer, Special Issue 9:141–148.

Balisky, A.C. and P.J. Burton. 1997. Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. New For. 14:63–82.

Bassman, J.H., J.C. Zwier, J.R. Olson, and J.D. Newberry. 1992. Growth of advance regeneration in response to residual overstory treatment in northern Idaho. West. J. Appl. For. 7:78–81.

Brang, P., J. Moran, P. Puttonen, and A. Vyse. 2003. Regeneration of *Picea engelmannii* and *Abies lasiocarpa* in high elevation forests of south-central British Columbia depends on nurse logs. For. Chron. 79:273–279.

British Columbia Ministry of Forests. 1990. Silviculture manual. Silv. Br., Victoria, B.C.

Butt, G. and A. Vyse. 1992. Regeneration of Engelmann spruce and subalpine fir in southern British Columbia following clearcutting. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Memo 210. http://www.for.gov.bc.ca/hfd/pubs/docs/Frm/frm210.pdf

Coates, K.D. 2000. Conifer seedling response to northern temperate forest gaps. For. Ecol. Manage. 127:249–269.

_____. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manage. 155:387–398.

Coates, K.D. and P.J. Burton. 1999. Growth of planted tree seedlings in response to ambient light levels in northwestern interior cedar–hemlock forests of British Columbia. Can. J. For. Res. 29:1374–1382.

Coates, K.D., S. Haeussler, S. Lindeburgh, R. Pojar, and A.J. Stock. 1994. Ecology and silviculture of interior spruce in British Columbia. For. Can. and B.C. Min. For., Victoria, B.C. FRDA Rep. 220. http://www.for.gov.bc.ca/hfd/pubs/docs/Frr/frr220.htm

Coupé, R., A.C. Stewart, and B.M. Wikeem. 1991. Engelmann Spruce–Subalpine Fir zone. *In* Ecosystems of British Columbia. D. Meidinger and J. Pojar (editors). B.C. Min. For., Victoria, B.C., Spec. Rep. Ser. 6, pp. 223–236. http://www.for.gov.bc.ca/hfd/pubs/docs/srs/srs06.htm

Coxson, D., S. Stevenson, and J. Campell. 2003. Short-term impacts of partial cutting on lichen retention and canopy microclimate in an Engelmann spruce–subalpine fir forest in north-central British Columbia. Can. J. For. Res. 33:830–841.

Day, R.J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. U.S. Dep. Agric. Dep., For. Publ. 1037.

_____. 1970. Shelterwood felling in late successional stands in Alberta's Rocky Mountain subalpine forest. For. Chron. 79(2):1970:380–386.

Delong, C. and D. Meidinger. 2003. Ecological variability of high elevation forests in central British Columbia. For. Chron. 79:259–262.

DeLucia, E.H. 1986. Effect of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. Tree Physiol. 2:143–154.

DeLucia, E.H. and W.K. Smith. 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. Can. J. For. Res. 17:527–533.

Eastham, A. 2001. Natural regeneration. *In* The Lucille Mountain Study: 8-year results of a silviculture systems trial in the Engelmann Spruce–Subalpine Fir zone. M.J. Jull and S.K. Stevenson (editors). B.C. Min. For., Res. Program, Work. Pap. 59. http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp59.htm

Eastham, A.M. and M.J. Jull. 1999. Factors affecting natural regeneration of *Abies lasiocarpa* and *Picea engelmannii* in a subalpine silvicultural systems trial. Can. J. For. Res. 29:1847–1855.

Eis, S. 1965. Development of white spruce and alpine fir seedlings on cut-over areas in the central interior of British Columbia. For. Chron. 41:419–431.

Farnden, C. 1994. Forest regeneration in the ESSF zone of north-central British Columbia. Can. For. Serv., Victoria, B.C. Info. Rep. BC-X-351.

Feller, M. 1997. Regeneration of Engelmann spruce and subalpine fir from seed in ESSFwc2 forests. *In* Sicamous Creek Silvicultural Systems Project: Workshop Proc. C. Hollstedt and A. Vyse (editors). Kamloops, B.C. B.C. Min. For., Res. Program Work. Pap. 24, pp. 154–169. http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp24.htm

_____. 1998. Influence of ecological conditions on Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) germinant survival and initial seedling growth in south-central British Columbia. For. Ecol. Manage. 107:55–69.

Fowells, H.A. (compiler). 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. For. Serv., Agric. Handb. 271.

Green, R.N., R.L. Trowbridge, and K. Klinka. 1993. Towards a taxonomic classification of humus forms. For. Sci. Monogr. 29.

Greene, D.F., J.C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29:824–839.

Huggard, D.J. and A. Vyse. 2002. Comparing clearcutting and alternatives in a high elevation forest: early results from the Sicamous Creek Project. B.C. Min. For., Res. Br., Victoria, B.C. Exten. Note 82. http://www.for.gov.bc.ca/hfd/pubs/docs/en/en82.htm

Klenner, W. and T.P. Sullivan. 2003. Partial and clear-cut harvesting of high-elevation spruce-fir forests: implications for small mammal communities. Can. J. For. Res. 33:2283–2296.

Knapp, A.N. and W.K. Smith. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Can. J. Bot. 60:2753–2761.

Krasowski, M.J. and J.R. Wang. 2003. Aboveground growth responses of understory *Abies lasiocarpa* saplings to different release cuts. Can. J. For. Res. 33:1593–1601.

Lajzerowicz, C.C., A. Vyse, M. Jull, and T. Newsome. 2006. Performance of planted Engelmann spruce and subalpine fir seedlings in British Columbia's southern mountains. For. Chron. 82:84–94.

Lajzerowicz, C.C., M.B. Walters, M. Krasowski, and H.B. Massicotte. 2004. Light and temperature differentially colimit subalpine fir and Engelmann spruce seedling growth in partial-cut subalpine forests. Can. J. For. Res. 34:249–260.

LePage, P.T., C.D. Canham, K.D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Can. J. For. Res. 30:415–427.

Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Can. J. For. Res. 24:934–944.

McCaughey, W.W., C.E. Fieldler, and W.C. Schmidt. 1991. Twenty-year natural regeneration following five silvicultural prescriptions in spruce-fir forests of the intermountain west. U.S. Dep. Agric. For. Serv., Res. Pap. INT-439.

McCaughey, W.W. and W.C. Schmidt. 1982. Understory tree release following harvest cutting in spruce-fir forests of the intermountain west. U.S. Dep. Agric. For. Serv., Res. Pap. INT-285.

Maser, C., S.P. Cline, K. Cromack, J.M. Trappe, and E. Hansen. 1988. What we know about large trees that fall to the forest floor. *In* From the forest to the sea: a story of fallen trees. C. Maser, R.F. Tarrant, J.M. Trappe, and J.F. Franklin (editors). U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. PNW-GTR-229, Chap. 2.

Mori, A., E. Mizumachi, T. Osono, and Y. Doi. 2004. Substrate-associated seedling recruitment and establishment of major conifer species in an old-growth subalpine forest in central Japan. For. Ecol. Manage. 196:287–297.

Newsome, T.A., M.J. Waterhouse, H.M. Armleder, and O.A. Steen. 2000. We're harvesting timber and maintaining caribou habitat: What about silviculture and other concerns? *In* Proc. From science to management and back: a science forum for southern interior ecosystems in British Columbia. C. Hollstedt, K. Sutherland, and T. Innes (editors). Southern Interior For. Extension and Res. Partnership, Kamloops, B.C. Res. Info. Rep. 1.

Noble, D.L. and R.R. Alexander. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the central Rocky Mountains. For. Sci. 23:420–429.

Oosting, H.J. and J.F. Reed. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. Ecol. Monogr. 22:69–91.

Owens, J.N. and M. Molder. 1985. The reproductive cycles of true firs. B.C. Min. For., Info. Services Br., Victoria, B.C.

Parish, R. and J.A. Antos. 2005. Advanced regeneration and seedling establishment in small cutblocks in high-elevation spruce–fir forest at Sicamous Creek, southern British Columbia. Can. J. For. Res. 35:1877–1888.

Puttonen, P., J. Kaipainen, and A. Vyse. 1997. Advanced regeneration in Engelmann spruce–subalpine fir forests. *In* Sicamous Creek Silvicultural Systems Project: Workshop Proc. C. Hollstedt and A. Vyse (editors). Kamloops, B.C. B.C. Min. For., Res. Program Work. Pap. 24, pp. 174–186. http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp24.htm

Roe, A.L. and G.M. DeJarnette. 1965. Results of regeneration cutting a spruce-subalpine fir stand. U.S. Dep. Agric. For. Serv., Res. Pap. INT-17.

SAS Institute Inc. 2003. Version 9.1. Gary, N.C.

Shearer, R.C. and J.A. Schmidt. 1999. Natural regeneration after harvest and residue treatment in a mixed conifer forest of northwestern Montana. Can. J. For. Res. 29:274–279.

Smith, H.J. and M.B. Clark. 1960. Growth and survival of Engelmann spruce and alpine fir on seed spots at Bolean Lake, B.C. 1954–59. For. Chron. 36:46–49.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry: the principles and practices of statistics in biological research. 3rd ed. W.H. Freeman and Co., New York, N.Y.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology 24:19–30.

Stathers, R.J., T. Newsome, M.J. Waterhouse, and C. Sutherland. 2001. Microclimate studies on a group selection silvicultural system in a high-elevation ESSFwc3 forest in the Cariboo Forest Region. B.C. Min. For., For. Sci. Program, Work. Pap. 58. http://www.for.gov.bc.ca/hfd/pubs/docs/wp/wp58.htm

Steen, O.A. and R.A. Coupé. 1997. A field guide to forest site identification and interpretation for the Cariboo Forest Region. B.C. Min. For., Victoria, B.C. Land Manage. Handb. 39. http://www.for.gov.bc.ca/hfd/pubs/docs/lmh/lmh39.htm

Steen, O.A., R.A. Coupé, H.M. Armleder, and R.J. Dawson. 2005. Development and structure of three high-elevation old spruce-fir stands in the Quesnel Highland of east-central British Columbia. B.C. Min. For., Res. Br., Victoria, B.C. Res. Rep. 26. http://www.for.gov.bc.ca/hfd/pubs/docs/rr/rr26.htm

Vyse, A. 1999. Is everything all right up there? A long-term interdisciplinary silvicultural systems project in a high elevation fir-spruce forest at Sicamous Creek, B.C. For. Chron. 75:467–472.

Wang, G.G. and K.J. Kemball. 2005. Balsam fir and white spruce seedling recruitment in response to understory release, seedbed type, and litter exclusion in trembling aspen stands. Can. J. For. Res. 35:667–673.

Waterhouse, M.J., R.B. Catton, and H.M. Armleder. 2004. Small mammal response to group selection silviculture systems in Engelmann spruce–subalpine fir forests. B.C. J. Ecosystems Manage. 3:121–135.

Weetman, G. and A. Vyse. 1990. Natural regeneration. *In* Regenerating British Columbia's forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston (editors). Univ. British Columbia Press, Vancouver, B.C., pp. 118–129.

Wright, E.F., C.D. Canham, and K.D. Coates. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. 30:1571–1580.

Wright, E.F., K.D. Coates, and P. Bartemucci. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Can. J. For. Res. 28:1352–1364.

Youds, J., J. Young, H. Armleder, C. Bauditz, M. Folkema, R. Hoffos, H. Knezevich, M. Lloyd, and M. Pelchat. 2000. Cariboo–Chilcotin Land Use Plan mountain caribou strategy. Cariboo Mid-Coast Interagency Management Committee. Williams Lake, B.C. Special Report.

Zhong, J. and B. van der Kamp. 1999. Pathology of conifer seed and timing of germination in high-elevation subalpine fir and Engelmann spruce forests of southern interior of British Columbia. Can J. For. Res. 29:187–193.